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Invasions of Puerto Rican Wetlands by the Australian Tree *Melaleuca quinquenervia*

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ABSTRACT.—Invasion theory suggests that the probability of an introduced plant displacing native flora and fauna is related, in part, to its performance in other climatically similar, non-native ranges. Herein, we sought to determine if the Australian native *Melaleuca quinquenervia*, an insidious weed in the wetlands of Florida USA, has also invaded similar habitats on Puerto Rico. Four naturalized populations of the exotic tree were discovered in environmentally sensitive Puerto Rican wetlands, including the Tortuguero Lagoon basin and San Juan Bay Estuary. Consistent with many plant invasions, the most probable seed sources for these naturalized populations are nearby ornamental plantings. Densities of the three *M. quinquenervia* populations studied in detail varied dramatically among sites, ranging from 2400 to 36000 trees per ha and fell within the range of stands observed in Florida. The number of capsular fruit produced per inflorescence is similar among Puerto Rico and Florida populations but markedly greater in comparison to its native range. In contrast, the number of seeds within fruits varied among stands and independently from geographic range. Unlike Florida, the rate of naturalization and the magnitude of invasion by *M. quinquenervia* is limited in Puerto Rico. We predict, therefore, that timely implementation of appropriate control tactics at this early stage of invasion with adequate follow-up efforts and continued vigilance will greatly enhance the probability of averting a large scale *M. quinquenervia* invasion in Puerto Rico.

KEYWORDS.—Invasive plants, naturalized populations, chemotypes, control strategies

INTRODUCTION

The myrtaceous tree *Melaleuca quinquenervia* (Cav.) S.T. Blake occurs naturally along Australia's eastern coast from Sydney in New South Wales to the northern tip of Queensland, in New Guinea, and in New Caledonia (Boland et al. 1987). Australian habitats that support *M. quinquenervia* populations typically include low-lying coastal wetlands behind heath-dominated headlands, riparian zones and brackish estuaries behind mangrove swamps (Rayamajhi et al. 2002a). Development in these areas threatens many *M. quinquenervia* dominated wetlands, which are located in highly desirable coastal areas of low topography, high rainfall, and mild climate (Turner et al. 1998; Boland et al. 1987).

Melaleuca quinquenervia has been internationally disseminated over the course of the last century for ornamental, revegetation, and agroforestry purposes (Turner et al. 1998; Serbesoff-King 2003; Dray 2003). It was introduced in the continental United States to California, Texas, and Louisiana, but it was most widely planted in Florida (Dray 2003). While not known to be invasive elsewhere, *M. quinquenervia* has proven to be a superior competitor to most, if not all, native vegetation occurring in the organically rich soils of forested and sawgrass dominated wetlands that characterize the Florida Everglades (Turner et al. 1998). After its introduction, *M. quinquenervia* spread at an estimated rate of 2,850 ha/yr (Center et al. 2000) and the weed now dominates ca. 200,000 ha of Everglades ecosystems (Turner et al. 1998). These *M. quinquenervia* wetland forests typically form dense monocultures characterized by continuous upper canopies with sparse under-

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stories (Rayamajhi et al. 2002a). Transitional stages of the invasion include savannahs with scattered, individual trees and mature dense stands surrounded by relatively pristine marshes that contain moderate to low levels of the tree (O'Hare and Dalrymple 1997).

Invasion theory suggests that the probability of an introduced plant becoming invasive is related to its performance in other climatically similar, non-native ranges (Reichard and Hamilton 1997; Kolar and Lodge 2001; Daehler et al. 2003). While the invasion and negative ecological impacts of *M. quinquenervia* are well documented in Florida (Serbersoff-King 2003), knowledge concerning the naturalization and performance of the tree in other climatically similar adventive ranges remains limited. *Melaleuca quinquenervia* has been planted widely, for instance, as an ornamental in Puerto Rico (USDA, 1995). When considering this tree's invasive nature in Florida, the abundance of suitable habitats, and its extensive use as an ornamental, we hypothesized that *M. quinquenervia* will also become invasive in the wetlands of Puerto Rico. Herein, we sought to 1) review the introduction history of *M. quinquenervia* in Puerto Rico, 2) quantify the geographic distribution of naturalized populations of the invasive tree on the island, 3) characterize the populations as compared to those of Florida as well as Australia, and 4) discuss methods of suppressing *M. quinquenervia* in Puerto Rico.

Materials and Methods

Surveys for naturalized populations of *M. quinquenervia* in Puerto Rico were initiated using a combination of herbarium searches, floristic inventories of wetland habitats, and informal assessments by natural area land managers. These efforts resulted in the enumeration of initially three naturalized populations of the tree, all occurring in the north-central region of the island (Fig.1). Determination of the stand's current geographic distribution was made by walking the perimeter of the stand while continuously recording GPS coordinates using real-time differential global positioning (GPS). Data at each site were collected in decimal degrees with resolution accuracy to the fourth decimal place. Data were imported into the geo-referenced software ArcView GIS version 3.2a (Environmental Systems Research Institute, Inc., Redlands, CA 92373) and graphical output was in the Mercator projection type.

We quantified the density and size-class distribution for each *M. quinquenervia* population by delineating several 100 m^2 plots at 50 m intervals along transects originating at the stand edge (smallest trees) and passing through the center of the stand (largest trees) in a stratified random design (Pratt et al. 2003; Van et al. 2002). The number of study plots varied according to stand size: three plots were delineated at the Tortuguero Lagoon site 1, while 5 plots were delineated at the remaining locations. The number of *M. quinquenervia* stems per plot and diameter at breast height (DBH, =1.3 m) of each individual was recorded (Van et al. 2002). Basal area per ha was calculated from DBH measurements, except in the case of trees <1.3 m in height, for which we measured stem diameter at the soil line. All other vegetation occurring in sample plots was tallied by species and percent coverage were recorded for both the arboreal canopy and understory strata.

Above-ground biomass estimates for *M. quinquenervia* were calculated by fitting DBH data from individual sites to the allometric model developed by Van et al. (2000):

$$Log_e\,(biomass) = -1.83 + 2.01 \times Log_e(DBH)$$

Trees <1.3 m in height and <1 cm DBH were excluded from the analysis. Caution should be used when drawing inferences from biomass estimates as the model is based on partitioned (allometric) measurements of *M. quinquenervia* trees growing in Florida and is not adjusted for possible differences in plant architecture, resource allocation, morphological variation, or other possible differences between Puerto Rican and Floridian populations.

Seed quantity and quality were assessed by destructively sampling 12 randomly se-

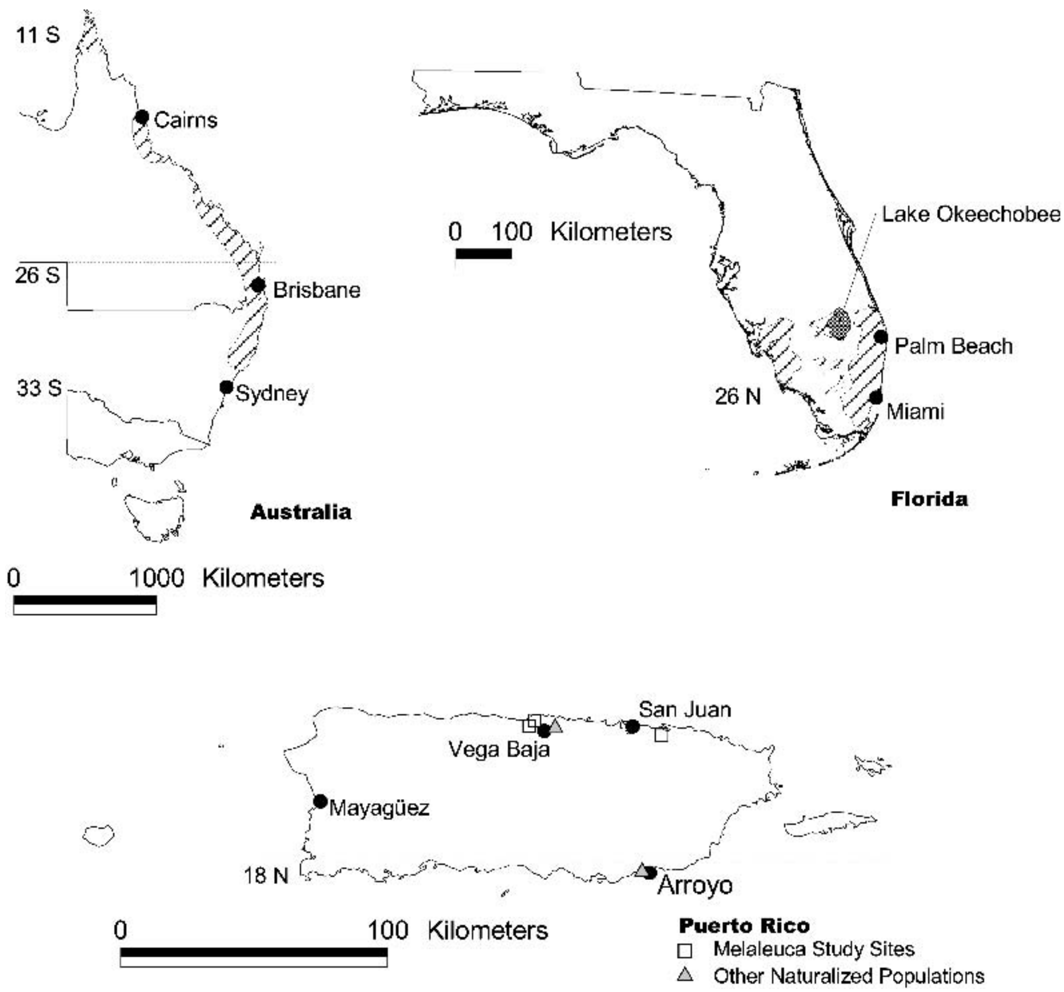

FIG. 1. Distribution of *Melaleuca quinquenervia* in its native Australian range and adventive ranges of Puerto Rico and Florida.

lected, reproductively mature trees at each study site. A randomly selected branch from each tree was harvested and the second infructescence (capsule cluster) from the branch apex was excised, placed into individual marked polyethylene bags and transported to the laboratory. Clusters located proximally on a branch are relatively older than those more distal due to auxotelic growth (Briggs and Johnson 1979). Adjacent clusters located on the same stem axis were considered distinct if they were separated by a series of leaves and/or leaf scars. The number of capsules per cluster was recorded. Three capsules were randomly selected from proximal, central and distal regions of each capsule cluster (n = 9 capsules per cluster), respectively, and placed into individual sealed glass vials. Capsules began to open and release seeds two days after collection. Seed parameters were assessed by evenly spreading the seeds from each capsule into individual petri dishes (5-cm diam; Microfiltrations Systems, Dublin, Calif.) containing a sterile filter paper as described by Rayamajhi et al. (2002b). Filter papers were soaked with 2 mL of 0.5% 2,3,5-triphenol tetrazolium chloride (TTC; Sigma Chemical Co., St. Louis), leaving a film of liquid on the surface. The dishes were closed and sealed with Parafilm®[i] and placed in a dark cabinet drawer for 7 d at 24°C (±2). Filled (embryonic) *M. quinquenervia* seeds appear black (nontransparent) when viewed with back lighting. However, seeds with living, respiring embryos stained red after soaking in TTC and were considered viable while non-viable seeds remained white to light pink (Rayachhetry et al. 1998; Grabe 1970). Seeds were considered germinable if they possessed an emerging radicle.

Capsule cluster and seed characteristics from Puerto Rican populations were compared to those from Florida and Australia as reported by Rayamajhi et al. (2002b). In general, we followed methods used by Rayamajhi et al. (2002b) except: 1) clusters were collected from trees occurring on the edge of mature stands and 2) only dry and seasonally flooded habitats were sampled. Comparisons of measured parameters among sites were analyzed with ANOVA and means were compared with a Tukey HSD test.

Florida populations of *M. quinquenervia* consist of two distinct chemical races (chemotypes) as measured by foliar terpenoid profiles (Dray 2003; Wheeler et al. 2002, Wheeler et al. 2003). To ascertain the chemotypes of trees invading natural areas in Puerto Rico we excised a single leaf from ca. 50 randomly selected trees per location, placed individual leaves into separate vials containing 95% EtOH, and transported the samples to the laboratory where they were frozen (−10°C) prior to terpenoid analysis. Samples were analyzed with an Agilent model 6890[i] gas chromatograph following the methods described by Wheeler (2004).

RESULTS

History of introduction

Earliest known records concerning the planting of *M. quinquenervia* in Puerto Rico date back to the first quarter of the twentieth century under the botanical synonym *Melaleuca leucadendron* (Britton and Wilson 1926). During those years, officers of the insular Department of Agriculture and Labor, the Federal Agricultural Experiment Stations on the island and its neighbor Saint Croix, as well as other private entities, were assiduously importing economic and ornamental species into local nurseries and gardens. Observations from the Puerto Rican plant survey conducted by Britton and Wilson (1926) from August 1923 through June 1926 described the occurrence of *M. quinquenervia* (referred to as cajeput) as "fine trees about 20 m high in the Mayagüez Experiment Station" (western Puerto Rico). Further investigations of Puerto Rican herbaria (UPR, UPRRP, SJ) elucidated reports and collection records documenting ornamental plantings of *M. quinquenervia* within the capital city of San Juan during the 1930-50s, particularly on lands administered by either local experiment stations or by the U.S. Forest Service, including the University of Puerto Rico, Rio Piedras arboretum. In 1960, the Agricultural Extension Service of the University of Puerto Rico included *M. quinquenervia* in a list of appropriate ornamental trees for small tracts of land and was identified as highly tolerant to wet soils, dry periods, strong winds and some degree of salt intrusion (Angleró 1960). *Melaleuca quinquenervia* was included within all published floras of Puerto Rico and the Virgin Islands for the last 30 years, consistently noted for its moderate use as a landscape tree with no mention of escape from intentional plantings (Little and Wasdworth 1964; Little et al. 1974; Liogier 1994; Liogier and Martorell 2000). Nonetheless, demand for the tree species in urban landscaping increased substantially island-wide from the 1980-90s, including its planting in public parks, promenades and along certain highway medians and green areas; private use on residential zones also increased during these years.

Naturalized populations

Naturalized *M. quinquenervia* populations were initially discovered and studied in detail at three locations on the island of

[i]Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture.

Puerto Rico. An additional stand was identified shortly before submission of this report but as little information is currently available we limit our discussion to the first three populations encountered. Based on preliminary field surveys and reports from land managers and environmental scientists, the current distribution of naturalized populations occurs primarily in the north central region of the island, with the exception of the newly discovered small stand in the southeast region near the town of Arroyo (Fig. 1). The climate in the north central region is humid and warm, with an average annual rainfall of 152.6 cm compared to the somewhat drier (88.0 cm) southern portion of the island. The warmest months are July and August with average daily maximum and minimum temperatures of 31.6 and 22.2°C, respectively. The coldest months are January and February with average daily temps of 23.3 and 23.5°C, respectively (Owenby and Ezell 1992).

Tortuguero Lagoon Basin.—Two naturalized stands of *M. quinquenervia* have invaded these wetlands, with additional scattered single trees dispersed in the vicinity of the primary stands. The first stand has invaded areas in the southern portions of the Tortuguero Lagoon Natural Reserve and the second occurs near the north eastern boundary of the reserve at a palustrine wetland known as Cabo Caribe, south of the town Vega Baja. Both sites are characterized by long hydroperiods and hydric Tiburones muck soils partially bordered by better drained soils (sandy loams or fine silicacious sand deposits). Historically Cabo Caribe wetland was partially drained, a series of irrigation canals were dredged, and the organic soils were farmed. Although the abandoned irrigation canals remain, restoration efforts have returned the area to a permanently inundated wetland dominated by *Typha domingensis* Pers. and *Cladium jamaicense* Crantz.

The first *M. quinquenervia* stand (site 1) was originally reported in 1995 and consisted of ca. 20 trees (Quevedo 1995). Shortly after its discovery, land managers cut trees near the soil level, resulting in stump coppicing and limited recruitment of seedlings. Currently, the stand is concentrated over a 638 m^2 area with isolated individual trees dispersed in the surrounding wetland. The stand is characterized by a dominance of reproductively mature trees at a density of 1.6 trees/m^2 (SD = 0.4) and an average DBH of 3.5 cm (SD = 3.84; DBH range = 0.01 to 21.2 cm; Table 1). Although it did not fall within our sampling plots, a large tree measuring 75 cm DBH was located near the stand's center. *Melaleuca quinquenervia*, covering 48.3% of the sampled area, was the only species occurring in the arboreal canopy stratum. The exotic tree also dominated (cover = 40%) the understory stratum, followed by *C. jamaicense* (10.5%), *Blechnum serrulatum* L. C. Rich (10%), and *Eleocharis mutata* (L.) Roemer and J. A. Schultes (9%), with the remaining species covering <1% of the plots.

The second, larger *M. quinquenervia* population (site 2) has invaded 1.3 ha of the sawgrass dominated wetlands. The stand is characterized by a predominance of widely dispersed, reproductively mature trees, with 0.24 stems/m^2 (SD = 0.21) and an average DBH of 9.2 cm (SD = 7.0; range = 0.02 to 32.8, Table 1). While the arboreal stratum was dominated by *M. quinquenervia* (24%), other tree species also occurred within the stand, including the exotic Australian native *Casuarina equisitifolia* L. (1%) and the native *Ficus stahlii* Warb. (0.2%). The dominant understory species was *C. jamaicense* (76%), followed by *M. quinquenervia* (8.8%) and *T. domingensis* (4%); the remaining species covering <1% of the stratum.

San Juan Bay Estuary.—The third *M. quinquenervia* population has invaded an herbaceous wetland, near the municipality of Carolina. This wetland drains into the Suarez Canal, which forms part of the San Juan Bay Estuary watershed. The site bears signs of historical development, as indicated by existing canals, and is characterized by organic soils, sands from plutonic origin, and a short hydroperiod (inundated <3 mos/yr). The invasive tree is distributed over 1.4 ha at a density of 3.6 stems/m^2 (SD = 4.1; Table 1), comparable to the highest population densities of the invasive tree observed in Florida. Van et al. (2002) reported density estimates ranging from 1.1 to 3.6/

TABLE 1. Stand densities and size distribution of the invasive tree *Melaleuca quinquenervia* in adventive habitats in Puerto Rico and Florida.

Site	GPS[a] coordinates	Hydroperiod[b]	Size (DBH) class distribution (cm)[c] 0-5	6-10	11-15	16-20	21-25	>25	Basal area (ha)	Plant density (ha)	Above-ground biomass (kg/ha)
Tortuguero Lagoon (site 1)	N −18.45566 W −66.43996	SF	129	19	8	2	3	0	34.0	16100	71.1
Tortuguero Lagoon (site 2)	N 18.47442 W −66.42080	PF	9	7	3	3	1	1	24.8	2360	52.1
San Juan Bay Estuary	N 18.42549 W −65.99397	SF	350	7	3	1	0	1	18.5	36160	38.4
Florida (2)[d]	N 26.05633 W −80.44016	NF	83	43	15	11	4	2	143.0	15800	263
Florida (3)	N 25.93178 W −80.44825	SF	206	45	18	12	4	1	148.8	28600	181
Florida (6)	N 26.16228 W −80.36269	PF	34	14	17	13	0	2	128.9	8000	149

[a]Global positioning system in decimal degrees (WGS84 datum).
[b]NF = non-flooded; SF = seasonally flooded (<6 months of the year); PF = permanently flooded.
[c]Number of individuals per 100 m^2 plot. Size class categories represent ranges in tree diameter at breast height (DBH = 1.3 m) measured in cm.
[d]Number in parentheses corresponds to study site reported in Table 2 of Van et al. 2000.

m^2 under similar hydroperiods in Florida. The size distribution along the sampled transect is presented in Table 1. Consistent with the previous locations, *M. quinquenervia* was the dominant arboreal species, covering 30.2% of the canopy stratum. Other tall shrub or tree species observed within the stand included *Sesbania sericea* (Willd.) Link and *Albizia procera* (Roxb.) Benth., each representing 0.2% of the arboreal or semiarboreal coverage. While *M. quinquenervia* (24%) constituted a large proportion of the understory vegetation, other taxa represented substantial components of this stratum, particularly grasses (43.8%) of several genera (*Paspalum millegrana* Schrad., *P. virgatum* L., *Sporobolus indicus* (L.) R.Br., and an unidentified sterile taxon probably of a third genus) and sedges (10.8%) represented by *Schoeneplectus americanus* (Persoon) Volkart ex Shinz & Keller, *Eleocharis mutata* (L.) R.& S., *E. geniculata* (L.) R & S., *Cyperus surinamensis* Rottb. and *C. polystachyos* Rottb. The composite *Wedelia trilobata* (L.) A.S. Hitch. a native of the neotropic, comprised 3.2% of the vegetation coverage, with the remaining species including the legume *Chamaecrista dyphyla* (L.) Greene and the endemic rubiaceous mound shrub *Mitracarpus portoricensis* Urban.

Chemotypes.—Foliar terpenoid profiles varied among sites. Trees from the second Tortuguero stand and the San Juan Bay Estuary site both contained nearly equal proportions of the two dominate terpenoids: 46%:54% and 54%:46% (nerolidol: viridiflorol), respectively. In contrast, the Tortuguero site 1 was dominated by the nerolidol chemotype: 96%:4%.

Reproductive characteristics.—The number of capsules within a cluster was greater in the tree's adventive range and did not differ among introduced locations (Table 2). The length of the clusters, in contrast, was similar among countries, with the exception of populations occurring in the permanently flooded habitats of the Tortuguero Lagoon, which possessed shorter clusters (Table 2). However, *M. quinquenervia* trees in adventive ranges possessed infructescences with higher capsule densities (number/cm) than those sampled in the tree's native range.

When pooling data from all Puerto Rican populations, distally located capsules within a cluster possessed slightly more seeds ($\overline{X}$ = 232.85 ± 12.89) than proximal capsules ($\overline{X}$ = 208.97 ± 9.34), with centrally located capsules intermediate ($\overline{X}$ = 219.67 ± 9.41; df = 2, 110; F = 3.01; P = 0.05). While statistically different seed densities exist among capsule regions, the biological relevance of these differences appears minimal. Capsule location within a cluster did not influence the viability (df = 2, 110; F = 1.98; P = 0.14), germinability (df = 2, 110; F = 1.41; P = 0.25) or embryonic status (df = 2, 110; F = 0.36; P = 0.70).

DISCUSSION

While it seems clear that *M. quinquenervia* can invade wetlands with hydroperiods like those sustained by sandy soils adjacent

TABLE 2. Seed characteristics of *Melaleuca quinquenervia* in its native and adventive ranges. Values represent averages (standard errors). Different letters indicate significant differences between treatment means (P < 0.05; Tukeys HSD).

	Australia[a]	Florida[a]	Tortuguero site 1	Tortuguero site 2	San Juan Bay Estuary	F	*P*
No. capsules	18.0 (0.9)a	49.0 (2.5)b	39.6 (2.1)b	41.9 (2.7)b	44.3 (2.9)b	61.61	<0.001
Cluster length	5.7 (1.6)a	6.0 (1.3)a	4.4 (2.2)b	4.4 (2.1)b	5.4 (2.6)a	4.68	0.001
Capsules/cm	3.0 (0.1)a	8.0 (0.3)b	9.0 (0.4)b	9.7 (0.7)b	8.2 (0.3)b	99.05	<0.001
No. seed	267.2 (11.8)ab	275.9 (6.3)a	165.5 (4.4)d	239.3 (6.1)bc	262.3 (12.9)ab	19.32	<0.001
% viable seed	3.5 (0.4)a	10.5 (1.6)b	10.2 (0.7)b	8.1 (1.0)b	4.2 (0.5)a	18.25	<0.001
% germinable seed	2.7 (0.3)c	9.9 (1.5)a	6.9 (0.8)b	3.4 (0.4)c	1.3 (0.3)c	24.89	<0.001
% embryonic seed	8.2 (0.6)c	14.3 (1.9)ab	18.8 (1.1)a	14.2 (1.6)b	8.2 (0.8)c	17.53	<0.001

[a]As reported by Rayamajhi et al. 2002.

to muck soils of Puerto Rico's northern coastal region, it is difficult to predict the total area at risk of invasion. In Florida, *M. quinquenervia* occurs abundantly within plant-hardiness zones 9a to 10b, corresponding with minimum temperatures of 1.7 to –3.8°C (Cathy 1990). These minimum temperatures, however, are much lower than those experienced in Puerto Rico's highest elevations. Like Florida, *M. quinquenervia*'s present distribution in Puerto Rico may be limited more by suitable habitat and propagule availability than by climate.

A more accurate predictor of the tree's potential distribution may be based on lands designated as wetlands and their proximity to a seed source. There are ca. 644,732,030.91 m^2 (64473 ha) of land meeting the estuarine and palustrine wetland classification in Puerto Rico, representing 7.2% of the island (Díaz and Rodríguez 2000). Consistent with Florida populations, our results suggest that those wetlands that experience moderate to short hydroperiods (as defined by Ewel 1990) are most vulnerable to invasion by *M. quinquenervia*. Consistent with many plant invasions, the most probable propagule sources for those naturalized populations described herein are nearby ornamental plantings of the invasive tree (Reichard and Hamilton 1997; Mack and Lonsdale 2001; Reichard and White 2001; Baskin 2002; Barton et al. 2004). Intentionally planted *M. quinquenervia* occurred <200 m from Tortuguero Lagoon site 1 and the San Juan Bay Estuary, with the third site occurring <1 km from existing trees. Similarly, Barton et al. (2004) determined that the invasion foci of several exotic woody species centered on intentional plantings in urban developments. Additional studies are needed to investigate the influence of local horticulture on recruitment and spread of *M. quinquenervia* in the wetlands of Puerto Rico.

In Florida, seed germination is limited or non-existent in habitats where water levels are maintained >0.5 m above the soil (Serbesoff-King 2003). However, *M. quinquenervia* seeds readily establish when droughts, development, or other factors reduce water levels, even for short periods of time. Therefore, one explanation for site variation in size class structure and recruitment patterns observed herein may be due to variation in hydroperiods among sites. At the Tortuguero Lagoon site 2, for instance, *M. quinquenervia* size classes are more uniform than those at the San Juan Bay Estuary, with the remaining site intermediate (Table 1). The recruitment of these trees likely occurred during a drought that was of sufficient magnitude to draw down the Cabo Caribe flood plain and allow appreciable levels of recruitment. In contrast, the variable hydrology at San Juan Bay Estuary does not appear to inhibit recruitment, resulting in a size (≈age) class distribution dominated by seedlings and saplings (Table 1).

Frequency and intensity of disturbance also influences *M. quinquenervia* size-class distribution (Rayamajhi et al. 2002a). Signs of fire, including scorched bark of large trees, were observed at each site and land managers at the Tortuguero Lagoon confirm that wildfires occur on a nearly annual basis. As a fire-adapted species with multilayered insulating bark, mature *M. quinquenervia* trees rarely suffer mortality from such disturbances. Fires of sufficient intensity, however, induce a massive seed rain from the canopy-held capsule clusters, resulting in high levels of recruitment under suitable hydrological conditions. In contrast to the other populations under study, the skewed size-class distribution at the San Juan Bay Estuary reflects the presence of numerous juvenile trees (DBH ≤5 cm) occurring on the invasion front of mature *M. quinquenervia* stands, representing >96% of the total number of trees in the stand (Table 1). The high regenerative capacity and successful recruitment at this site underscores the invasion potential of *M. quinquenervia* under these variable hydroperiod and periodic disturbance regimes.

Foliar terpenoid profiles varied considerably among sites. Our results suggest that, although the Tortuguero Lagoon sites are in close proximity (~3 km), gene flow is limited, resulting in chemotype maintenance at site 1. These findings are consistent with restricted gene flow patterns in Florida, where chemotype profiles also varied dramatically among stands irrespective of proximity (Dray 2003). These trends in gene flow restrictions may be related to life history characteristics of the invasive tree. The minute *M. quinquenervia* seeds, for instance, are gravity-dispersed and deposited within a short distance (<170 m) of the parent tree (Meskimen 1962; Browder and Schroeder 1981). In addition, honey bees (*Apis mellifera*) are the principle pollinators of the tree in Florida (Vardaman 1994). Hamrick et al. (1979) indicate that social insects provide limited pollen dispersal for many plant species. These factors, in addition to the human-aided transportation of plant material, may explain the restricted exchange of genetic material observed among *M. quinquenervia* stands (Dray 2003).

These data demonstrate that capsule cluster length, and by inference inflorescence length, does not differ appreciably among adventive and native ranges studied herein but the number of capsules arising from these flowers is markedly increased in introduced ranges (Rayamajhi et al. 2002b). One explanation for these results is that *M. quinquenervia*, in the absence of top-down regulation from herbivores, is able to maximize allocation of resources to reproduction rather than replacement of damaged tissues or defense (Willis et al. 1999). Following this logic, we also hypothesize that *M. quinquenervia* trees in adventive ranges not only possess greater densities of capsules per cluster but also greater numbers of clusters per tree.

In contrast to trends in capsule densities, the number of seeds within a capsule varied among sites and independently from geographic range (Table 2). Seed densities per capsule were similar among Australia, Florida and San Juan Bay Estuary populations yet lower for the Tortuguero Lagoon site 1, with site 2 intermediate (Table 2). The latter populations occur in long-hydroperiod systems, suggesting that the number of seeds per capsule may decrease with increases in hydroperiod. However, seed viability, germinability and embryonic status of seeds were generally greater in Florida and permanently flooded sites in Puerto Rico than in Australia and San Juan Bay Estuary (Table 2). Additional studies are needed with greater levels of replication to determine how hydroperiod influences seed quantity and quality.

Control strategies

Strategies for controlling invasive weeds often include early detection of incipient populations, timely implementation of appropriate control measures and continued monitoring after local removal. As described above, time since establishment and the magnitude of *M. quinquenervia* invasion is limited in Puerto Rico. In addition, multiple control tactics are available to combat the invasive tree, with varying levels of efficacy and appropriateness (Laroche 1999). We predict, therefore, that 1) timely implementation of control tactics at this early stage of invasion with 2) adequate follow-up efforts and 3) continued vigilance will greatly enhance the probability of averting a large scale *M. quinquenervia* invasion in Puerto Rico. Here we describe *M. quinquenervia* control measures and address their appropriateness for the specific sites.

Physical control.—Physiological stress, and in some cases death, of *M. quinquenervia* trees has resulted from environmental alterations in hydroperiod and fire. *Melaleuca quinquenervia* is a fire-adapted species and therefore prescribed burns must be used cautiously, with care given to the proper timing of treatments so as to coincide with unfavorable conditions for seedling recruitment (Laroche 1999; Serbesoff-King 2003). However, multiple recent wildfires have had little apparent impact on the *M. quinquenervia* population at Tortuguero Lagoon basin sites and are likely facilitating the prolific recruitment of seedlings at the San Juan Bay Estuary site. The suitability of prescribed burns at the latter site is also questionable due to the urban development surrounding the natural area.

Manipulation of hydroperiod alone has not been shown to be an effective tool for suppressing existing *M. quinquenervia* trees. Mature and sapling trees have the ability to withstand prolonged periods of inundation. However, increasing or maintaining high water levels may play an important role in limiting recruitment of *M. quinquenervia* seedlings. While the maintenance of extremely long periods of high water may reduce the numbers of seeds germinating, this alteration in hydroperiods in natural areas may also have adverse affects on native plants and animals (Lockhart 1999).

Herbicidal control.—The most effective approach for managing *M. quinquenervia,* which produces the most rapid results, is the use of herbicides. Two commonly used approaches for removal of large individuals involve girdling the trunks and applying herbicide into the injury or felling trees and treating the stump. Herbicide is applied directly onto the exposed cambial layer of girdled trees, resulting in mortality of above and below ground portions of the tree. Stumps of felled *M. quinquenervia* trees readily coppice if left untreated and cut stems must be suspended above the water level to avoid development of adventitious roots. The cost associated with treating *M. quinquenervia* using manually applied herbicides in Florida is estimated at US$ 4500/ha (Laroche and McKim 2004). However, these estimates were developed from mature stands with greater biomass (111.7 metric ton/ha) than those occurring in Puerto Rico. Using this conservative estimate, we approximate herbicidal treatment costs at US$315, 5850, and 6300 for Tortuguero site 1, Tortuguero site 2, and San Juan Bay Estuary, respectively (F. B. Laroche pers. com.). Like any disturbance, chemical control strategies for *M. quinquenervia* are complicated by the canopy-held seed bank, which is liberated when vascular tissues are disrupted (Rayamajhi et al. 2002a). Therefore, manual removal of seedlings is required two years after initial treatment (see below), which will inflate these initial costs. Expansive monocultures (>50 ha), which to our knowledge do not currently exist in Puerto Rico, can be treated aerially but this method is not appropriate for use on small stands because of the impact to native plant communities.

Mechanical and manual control.—Felling trees and manual removal of seedlings or small saplings are the only forms of mechanical control that are currently recommended for use in natural areas of South Florida (Laroche 1999). Although time consuming, hand removal of saplings can be an effective method of controlling seedlings and saplings <1 m in height. Mechanical removal of *M. quinquenervia* using heavy equipment often results in unacceptable levels of collateral damage to native vegetation and soil systems. However, the use of heavy equipment in accessible areas, such as along canals, utility rights-of-way, and in new developments has been applied (Laroche 1999).

Biological control.—Classical weed biological control involves reuniting an invasive plant with coevolved natural enemies from its native range. Reestablishment of top-down regulation through the introduction of specialized herbivores has been demonstrated as an effective method of controlling *M. quinquenervia* in Florida. The first candidate selected for quarantine based host range testing and risk assessment was the Australian weevil *Oxyops vitiosa* Pascoe (Purcell & Balciunas 1994). Prerelease studies indicated that the weevil would exploit only a very narrow range of myrtaceous species in the *M. leucadendra*-complex, none of which are native to the Americas (Balciunas et al. 1994). *Oxyops vitiosa* was subsequently released at melaleuca-infested locations in 1997 and has established throughout southern Florida (Pratt et al. 2003), except at sites with long-hydroperiods where the subterranean pupae cannot survive prolonged submergence (Center et al. 2000). Herbivory from the weevil results in 80% reductions in reproduction, delays reproductive maturity, and reduces growth rates of the invasive tree (Pratt unpublished data). The second herbivore introduced for biological control of *M. quinquenervia* in Florida was the melaleuca psyllid, *Boreioglycaspis melaleucae* Moore. Host specificity testing demonstrated that the herbivore would only complete development on two *Melaleuca* species: *M. quinquenervia* and *M. viridiflora* (Gaertn.) and was subsequently established in South Florida in 2002 (Wineriter et al. 2003). Both adults and nymphs feed on expanding buds and leaves but as competition for these sites increase, nymphs also exploit mature, fully expanded leaves. Preliminary data have shown that feeding by psyllids results in 60% mortality of seedlings within three generations of the insect (Pratt unpublished data).

The feasibility of implementing a biological control program for *M. quinquenervia* in Puerto Rico is dependent, in part, on 1) the host specificity of the existing biological control agents in relation to the island's flora and 2) conflicts of interest inherent in targeting ornamentally planted *M. quinquenervia* trees. The biological control agents approved for introduction into Florida, for instance, have not been evaluated as to their propensity to oviposit and develop on Myrtaceae of Puerto Rico and the Virgin Islands. Liogier (1994) cites 30 species in the family Myrtaceae that are native to the island of Puerto Rico, none of which were included in initial host testing for the biological control agents described above. In addition, there are four federally endangered Myrtaceae in Region 4 (U.S. Virgin Islands and Puerto Rico) of the United States Fish and Wildlife Service: *Calyptranthes thomasiana* Berg, *Eugenia haematocarpa* Alain, *Eugenia woodburyana* Alain, and *Myrcia pagani* Krug and Urban. These species, as well as representatives from the other native Myrtaceae and closely related economically important flora, must be evaluated prior to requesting permission to introduce the herbivores into Puerto Rico.

The self-perpetuating and dispersing qualities of intentionally introduced herbivores are often characterized as beneficial aspects of classical weed biological control. After introduction, however, biological control agents of *M. quinquenervia* will exploit ornamental plantings of the targeted species and invasive weed populations alike. While reductions in reproduction of intentionally planted trees will limit continued invasion of environmentally sensitive wetlands, decline in the aesthetic quality of ornamental *M. quinquenervia* trees by the introduced herbivores is likely to be met with some public resistance. Therefore, conflicts of interest between the issues of halting continued invasion of wetlands and maintaining ornamental plantings must be addressed prior to implementing a biological control program for *M. quinquenervia* in Puerto Rico.

In Florida, it was determined that an integration of all available control techniques is required to effectively eliminate *M. quinquenervia* from natural areas (Laroche 1999). The overall philosophy of integrated control methods is to suppress invasive weeds through a combination of biological, physical, and chemical methodologies that reduce pest populations to acceptable levels while minimizing impacts on the environment. This strategy, however, was developed under the realization that *M. quinquenervia* was widely distributed over vast natural areas that were difficult to access so eradication of naturalized populations was unfeasible (Laroche 1999). In contrast, the geographic distribution of the invasive tree in Puerto Rico is limited, so cost-effective herbicides can halt existing invasions.

When considering its broad use as an ornamental, it is doubtful that naturalization and invasion of *M. quinquenervia* is limited to Puerto Rico and Florida. Ornamental plantings of the exotic tree also occur on St. John in the Virgin Islands, the Dominican Republic, San José, Costa Rica, and anecdotal reports from the Zapata Península in Cuba as well as Cuernavaca, México. It remains unclear, however, if *M. quinquenervia* is spreading beyond these intentional plantings into nearby environmentally sensitive lands of the West Indies and Central America. Collaborative efforts to conduct field surveys, herbarium searches, and improved communication among natural area managers would greatly enhance efforts to limit the ecological damage by this and other invasive plants. Finally, the development of models that accurately predict the plants geographic distribution may greatly facilitate these endeavors.

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